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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE
MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE.
E. L. MARK, DIRECTOR.—No. 127.

*STUDIES ON THE REACTIONS OF LIMAX MAXIMUS
TO DIRECTIVE STIMULI.*

BY PETER FRANDSEN.

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INTRODUCTION.

THE following studies were made at Harvard University during the fall and winter of 1898-99. The problem was proposed by Dr. C. B. Davenport and the investigation carried on under his immediate direction. I wish here to acknowledge my indebtedness to his many suggestions and helpful criticisms throughout the year. In connection with the preparation of the manuscript for publication, I am under obligation to Dr. E. L. Mark for many kindnesses.

The behavior of any organism toward artificial stimulation is probably always largely dependent on its normal environmental conditions. The long action of those conditions, assisted, perhaps, by the animal's own efforts, conscious or unconscious, to adapt itself to them, finally results in certain habits and instincts. The process of adaptation being extremely slow, organisms are strongly averse to great or sudden changes in their environment and incapable of adjusting themselves to them. As a rule, then, we should expect animals to seek those conditions of light, heat, moisture, and other physical and chemical influences which are most in accordance with those to which they are normally subjected.

The most easily observed responses of animals are naturally those which find their expression in locomotion. The number of stimuli which may influence locomotion are, of course, numerous, but of these a certain limited number play much the larger part. If we had an accurate knowledge of the relative weight of these different forces, we might predict with certainty the path any animal would follow under certain given conditions. An experimental study of the different stimuli ought at least to enable us to find out which ones do operate, and perhaps to establish certain general laws regarding them and the biological tendencies which impel the animal to respond.

The present paper is a study of the locomotor responses of the slug *Limax maximus* to three kinds of stimuli, — those of touch, gravity, and light. In connection with these studies new problems have constantly arisen, some of which have been cursorily considered, many others merely alluded to, so that the work is far from being complete.

The term "geotaxis" has been used to designate the influence of gravity on locomotion. Interesting and careful studies have been made on the geotaxis of numerous Protista by Schwarz ('84), Aderhold ('88), Massart ('91), and Jensen ('93). These investigations clearly show a geotactic response in the unicellular organisms studied. The kind of response varies according to other conditions, such as those of light, heat, density of medium, chemical influences, etc., and may also differ in individuals of the same genus under apparently like conditions. Massart ('91, pp. 161-162) found that, when a number of *Spirilla* were put into a vertical tube, one group collected in the upper part and another at the lower part. He also found (p. 164) that *Chromulina woroniniana* was negatively geotactic — that is, moved upward, or in a direction opposite to that of the pull of gravity — at 15° to 20° C., but positively geotactic at 5° to 7° C. Jensen's work also showed the important influence of other agents in modifying geotaxis. Loeb ('88, pp. 7-8) found that cockroaches preferred the steepest side of a box whose four sides were inclined at different angles; that is, they are negatively geotactic. He also discovered that a number of other Metazoa were geotactic.

In a certain way, the present paper is a continuation of a recent study made by Dr. C. B. Davenport and Miss Helen Perkins on geotaxis in the slug. Davenport and Perkins ('97, p. 105) discovered that the intensity of the animal's geotactic response was directly proportional to the sine of the angle of deviation from the vertical, and hence "varied directly as the active component of gravity." In the third section of their paper, the question, "What determines whether the head end of

the slug shall be directed up or down?" was raised and considered. The results showed that certain individuals appeared to have a fairly marked positive geotaxis, for, when placed on an inclined glass plate, such animals swung the head-pole of the axis toward the earth; but others showed as strongly marked a tendency to move away from the earth, and a few seemed indifferent as to whether they went up or down. Their experiments showed further that there was, apparently, no inherent tendency in individual animals to move either to the right or to the left, so that the difference in geotactic response could not be explained as due to differences of an inherent tendency of this kind. The effect of a slight initial impulse given to the head of the animal indicated that the thigmotactic, or contact, stimulus imparted to the animal in handling might, to some extent, modify its response to the stimulus of gravity. But Davenport and Perkins did not reach any definite, satisfactory answer to the main question.

It was to test their observations by a larger number of experiments, and, if confirmed, to explain them by further experimentation, that the present investigation was undertaken. In the first place, I wished to find out whether certain individuals, if put on an inclined glass plate, always responded to the pull of gravity by directing the head end up and moving away from the earth, and whether certain other individuals always did the contrary. If this proved to be true, then it was my main problem to seek the reason for it. Is the force which makes some slugs go up, others down, and still others indifferent to the attraction of gravity, a purely accidental one, — is it a physical force, or is it what we may call a psychical peculiarity, which varies in different individuals and in the same individual at different times? As a preliminary to the main problem, I first made a series of experiments on the animal's thigmotaxis, — its response to contact- and pressure-stimuli. By virtue of its thigmotaxis, an animal moves either toward or away from the agent which comes in contact with it, just as its geotaxis is expressed in a movement toward or away from the earth, in response to the attraction of gravity.

I. THIGMOTAXIS.

Material and Methods. — The animal used in all the following experiments was *Limax maximus*, which is fairly abundant in the greenhouses about Cambridge. Material was obtained from several different greenhouses and kept in a large closed tin box, the bottom of which was covered with moss kept moist, so as to afford an environment as much like the customary one as possible. Fresh cabbage leaves constituted the

animal's main food. The cannibalistic tendencies of the slug, together with an unavoidable deterioration due to repeated handling, necessitated a frequent renewal of the animals.

The methods used in the experiments were simple. The slug was placed on a circular glass plate set horizontally in the bottom of a cuboidal wooden box which was made impervious to light and covered with a thick, black cloth. Precautions were taken to avoid thermal and chemical influences by keeping the box at as equable a temperature as possible and by wiping the plate free from slime before each test. The tests were made only when the animal had definitely oriented itself and was moving ahead in a straight line. Two series were made. In the first series the dorsal tentacle was touched gently with the forefinger. The box was then immediately covered with the black cloth. Observations were made after the lapse of 20 to 30 seconds and the position of the animal noted. The right and left tentacles were touched alternately.

Results. — The following Table (I.) gives the results of a number of experiments on ten different animals.

TABLE I.
RESPONSE TO THIGMOTACTIC STIMULATION OF THE TENTACLES.

Animal No.	Number of Trials.			Total Number of Trials.
	—	+	0	
1	7	2	3	12
2	11	3	3	17
3	8	3	1	12
4	4	3	3	10
5	7	2	0	9
6	6	0	2	8
7	10	2	2	14
8	16	4	2	22
9	18	1	5	24
10	22	1	4	17
Totals . .	99	21	25	145

The column headed with the minus sign shows the number of times the animal responded by moving *away* from the source of stimulus; the one headed with the plus sign, the number of times it moved *towards* that source; and the zero column, the number of times there was *no* response. I found that the animal would respond very definitely and precisely to stimuli two or three times in succession by immediately retracting the tentacle touched and moving away from the stimulating influence. After the third trial, however, it either refused to change its direction of locomotion or else moved directly towards the source of the stimulus. If a respite of a few seconds before the next stimulation was then permitted, the animal would again give a precise negative response for two or three trials, and then, as before, it desisted. Out of the total 145 tests, there was a negative response in two thirds of the trials. The remaining trials — one third of the whole — were about equally divided between the positive responses and refusals to respond at all. Sometimes five or six tests were made in quick succession, so that the total negative response is rather less than it would have been if a rest had been given in each case after three tests. Out of the 21 cases of direct positive response, 15 were cases where the right tentacle was touched, and the remaining 6 were due to stimulation of the left tentacle. Similar, but more marked, differences between the results of stimulating the right and the left tentacles were observed in other experiments. This suggests that either the right tentacle may be less sensitive to stimuli, or that its counterirritancy may be more readily aroused. There is, however, a third possible cause. The animal may have an innate tendency to go to the right, and, if so, this tendency may diminish to some extent the force of the stimulating agent when it impinges on the right side of the animal, and correspondingly increase the response when the stimulus is directed upon the left side of the animal. Something further will be said about this point in a later part of the paper.

A few thigmotactic experiments were next made on the sides of the animal posterior to the head. The right and left sides were touched alternately. The results are given in Table II.

Phenomena like those observed in stimulating the tentacles are seen here, and they also agree with similar observations by Davenport and Perkins ('97, p. 109.) After two or three trials, the animal begins to show resistance, and if the finger is held against its side, will sometimes try to displace the finger by pushing against and curling the body around it. The frequency of the negative response is here somewhat less marked than in the preceding experiments, which is as we should expect, owing

to the greater sensitiveness of the tentacles as special tactile organs. In these experiments every one of the minus and zero results was due to stimulation of the right tentacle.

TABLE II.

RESPONSE TO THIGMOTACTIC STIMULATION OF THE SIDES OF THE BODY.

Animal No.	Number of Trials.			Total Number of Trials.
	-	+	0	
1	11	3	3	17
2	8	6	2	16
3	17	5	4	26
Totals . .	36	14	9	59

These facts clearly prove that, under ordinary circumstances, the slug is negatively thigmotactic. In our consideration of the animal's responses to other stimuli, we shall have to take this into account, as causing occasional vagaries, and therefore endeavor to eliminate it as much as possible from the experiments.

II. GEOTAXIS.

What determines whether the head end of the slug shall be directed up or down?

Methods.—The same apparatus was used as in the preceding experiment. A circular glass plate was employed so that the animal could be rotated into any desired position without the necessity of its being handled. The plate was set in a box at an angle of about 45° with the horizon. In each test the animal was so placed on the plate that the long axis was horizontal, different sides being directed downward in different trials. At first the experimentation consisted mostly of watching the animals in order to obtain some clue for further work. Later, rough sketches of the pigment patterns of the individual animals were made, so that it was possible to identify individuals with certainty; the same animal could then be subjected to experiments at different times and the difference in results noted. The methods used in working out particular

questions will appear as these questions are considered. As the same number of experiments were not made on each animal studied, I have, for the sake of comparison, estimated in each case the geotaxis in per cents. This percentage is obtained by dividing the number of positive or negative responses by the total number of responses. The nearer the geotaxis percentage approaches 100 the more precise has been the kind of response. No fixed time was allowed to elapse between successive tests, but in each test the observation was made at an interval of from 30 to 60 seconds after covering the box.

Operations and Results. — The first question investigated was whether particular animals exhibited a decisive positive or negative geotaxis. A number of tests were, therefore, made on each of several selected individuals. The results obtained were like those of Davenport and Perkins ('97, p. 108); that is, certain animals showed a very marked positive geotaxis; others, an equally decided negative tendency; and a few, perhaps one animal out of 12 or 15 where 10 or more tests were made, were apparently geotactically indifferent. The occasional irregularities in the responses of individual animals were easily seen to be due to influences other than pure gravity, such as jarrings of the plate, influence of contact in putting the animal on the plate, and to the influence of light admitted in lifting the cover of the box. Frequently, upon the raising of the cloth to make an observation, the animal would retract its tentacles, as if dazzled by the sudden inflow of light, and at the next observation it would be seen to have altered its response.

Naturally, this question next arose, Is the response the same on different days? In Table IV. (p. 195) are given the results with a number of animals experimented on to test this point. These are numbers 2, 7, 8, 22-25, 27. Number 2 was positively geotactic on two days and negative on another day. A similar variation is seen in the case of slugs 7 and 22. In the case of all the rest, however, there is a very marked constancy. The ninth (last) column in the table indicates the condition of the animals at the time of experimentation. We see from this that on the days of different response, the animals were in somewhat unlike conditions, which may account for the irregularity of response. The significance of this will be dealt with later. The important matter here is, that the animals, when in the same condition and under the same circumstances, have a fairly constant geotaxis from day to day. One of the most marked cases is that of number 24. This animal was experimented on at different times for a period of three weeks. During this period, it was always active and in good condition, and, as the

table shows, at all times, exhibited nearly the same percentage negative geotaxis. At the last trial made, it responded irregularly, and so slowly, — at one time not changing its position for thirty minutes, — that I had to give up the attempt to obtain a series. This was often the case with other individuals after a few definite responses.

Tests were then made on the geotaxis of the same individuals at different times of the same day. Considering the slug's normal environment, it would not be surprising if, for instance, it should show an upward tendency in the evening and a downward geotaxis in the daytime. Its nocturnal habits and dislike of daylight might give it a different geotactic instinct at night from that of the daytime. I insert here a table (III.) giving the results of a few experiments bearing on this point. As the table shows, the response is pretty constant at different

TABLE III.

GEOTAXIS OF THREE INDIVIDUALS AT DIFFERENT TIMES IN THE DAY.

Animal No.	Time of Day.	Number of Trials.		% Geotaxis.	Condition of Mucus.
		+	—		
1	8.00 A.M.	5	2	+71.4	Good
	1.30 P.M.	6	3	+66.6	Rather Dry
	8.30 P.M.	7	4	+68.6	Tail Dry
2	1.30 P.M.	16	1	+94.1	Good
	7.00 P.M.	9	18	-66.6	Rather Dry
	7.00 P.M.	12	5	+70.5	Fair
	10.00 P.M.	6	3	+66.6	Fair
3	7.00 A.M.	3	8	-72.7	Fair
	1.30 P.M.	0	5	-100.	Fair

times of the same day. The one exception is number 2. That it was negative on one evening at 7 P. M., may be explained by the fact that its condition was not good. Moreover, on another evening at the same time the animal had become positively geotactic.

From the observations recorded in Tables III. and IV., it is plain that the geotactic response is not due to purely accidental factors, but can

be explained only by some marked difference between the individual animals. The first thought is that differences in response are due to a difference in size, and the facts seem to give some support to that explanation. Most of the positively geotactic individuals were found among the small and medium-sized animals, and nearly all the negative animals were of large size. Moreover, the few indifferent individuals were of medium size. This, however, was not an invariable rule. Small animals were sometimes negatively geotactic and, occasionally, a large slug would migrate earthward.

A second, clearly important, factor is the condition of the animal's mucus. As shown by the preceding experiments, animals, positively geotactic when normal, became negatively geotactic when lacking in an abundance of sticky slime; *e. g.* animal 2, Table III., and animals 2 and 7, Table IV. On the other hand, in one instance (22 b), a negative animal, when extremely sticky, went downwards. Abundant, sticky mucus is evidently connected with a downward migration, and dryness seems to force the animal to take an upward direction. But these facts are not enough to explain all responses. For sometimes two animals of nearly the same size and in equally good condition gave different geotactic responses. We must look for other differences. It will, however, be necessary first to refer briefly to the form and external appearance of the slug.



FIGURE 1.

Outline of *Limax maximus*. *mtl. a.*, anterior edge of mantle; *mtl. p.*, posterior edge of mantle; *a. to mtl. p.*, anterior region of body; *mtl. p. to p.*, posterior region; *oc.*, eye; *ta. d.*, dorsal tentacle; *ta. v.*, ventral tentacle; *of. pul.*, pulmonary orifice.

The slug, if we except the respiratory opening on the right side of the body, is externally bilaterally symmetrical. It has no external shell. There are two pairs of tentacles,—a dorsal pair bearing the eyes and a smaller ventral pair. The mantle extends from the neck, ventrally, to near the edge of the foot. Posteriorly, it forms a prominent fold, as indicated in the figure, which may be used to separate the body into an anterior and a posterior region. Observations of the animal

reveal that it has very different degrees of control over these two regions of the body. In locomotion, the head end of the body, back as far as the respiratory opening, is freely swung about from side to side and determines the axis of orientation of the animal. Over the posterior region, the animal seems ordinarily to have very imperfect control. The relation between the two regions is crudely that of a span of horses to a chain of wagons which they are pulling. When the horses change direction, the wagons come only slowly around into position one after the other, and there is likely to be some slipping in the process, especially if it takes place on a down grade. In watching the slug, I saw that the adhesion of the anterior region appeared considerably greater than that of the posterior. When the animal gets dry, it does so first at the posterior region. The tip of the tail is the part first to lose its clinging power, and it may curl up dorsally as a result of the drying process. If an animal which is thus beginning to deteriorate in its supply of mucus be put on a glass plate and the plate raised into a vertical position, the slug will move along and desperately cling to the plate with the anterior part of its body. The posterior region will gradually swing downward as a result of the pull of gravity, and, in consequence, the animal's head will eventually be directed upward. From this, we are justified in concluding that the same principle will operate, although to a considerably less degree, in the animal's normal condition. A hasty examination showed that there was a good deal of variation in the proportions of the two regions in different individuals. As a crude and easy way of estimating these proportions, I measured the length in millimeters of the anterior region from the tip of the head to the posterior fold of the mantle, and similarly the length of the posterior region from that fold to the tip of the tail.*

The results from 27 animals thus measured are given in Table IV.

The individuals (Table IV.) are arranged in a series, beginning with those in which the two regions are most nearly of the same length and ending with those in which the disproportion is greatest. In animal No. 1, the length of the anterior region is 83.3 per cent (column 8) of the posterior; that is, the ratio is almost one to one. In No. 25, the anterior region is only 45 per cent as long as the posterior, or less than half its length.

The fifth column in the table gives the geotaxis of individuals in per

* The measurements were made when the animal was extended and moving across the plate. The amount of elongation varies a good deal, but the regions retain pretty closely their relative proportions.

TABLE IV.

SUMMARY OF GEOTACTIC RESULTS.

Animal No.	Series of Observations on Different Days.	Number of Trials.		% Geo-taxis.	Length of Anterior Region in mm.	Length of Posterior Region in mm.	Ratio of Ant. to Post. Region in per cents.	Condition of Animal.
		+	—					
1	. . .	10	0	+100.	20	24	83.3	Good.
2	a	6	3	+ 66.6	18	22	82.	Fair.
2	b	5	18	— 72.2	18	22	82.	Dry.
2	c	12	5	+ 70.5	18	22	82.	Good.
3	. . .	6	0	+100.	6.5	8	81.	Good.
4	. . .	6	1	+ 85.7	17	21	81.	Good.
5	. . .	5	2	+ 71.4	24	30	80.	Good.
6	. . .	7	1	+ 87.5	11	15	73.	Good.
7	a	0	4	—100.	26	40	65.	?
7	b	9	6	+ 60.	26	40	65.	Rather dry.
7	c	7	3	+ 70.	26	40	65.	Slow.
7	d	0	2	—100.	26	40	65.	Tail slips.
8	a	12	6	+ 66.6	?	?	?	Good.
8	b	17	1	+ 94.4	?	?	?	Good.
9	. . .	0	6	—100.	21	33	63.6	Tail slips.
10	. . .	2	8	— 80.	20	32	62.	Mucus watery.
11	. . .	14	3	+ 82.3	21	34	61.8	Good.
12	. . .	6	0	+100.	27	44	61.	Good.
13	a	5	12	— 70.5	17	25	61.	Active.
13	b	3	8	— 72.7	17	25	61.	Active.
14	. . .	9	3	+ 75.	20	33	60.5	Good.
15	. . .	1	8	— 88.8	24	40	60.	Fair.
16	. . .	0	10	—100.	23	50	56.	Good.
17	. . .	6	14	— 70.	30	55	54.5	Good.
18	. . .	8	3	+ 72.7	30	56	53.5	Extrem'ly sticky.
19	. . .	0	8	—100.	23	43	53.5	Fair.
20	. . .	1	5	—88.3	17	32	53.	Good.
21	. . .	4	12	— 75.	21	40	52.5	Good.
22	a	7	8	— 53.3	41	79	52.	Sticky.
22	b	8	5	+ 61.5	41	79	52.	Very sticky.
23	a	5	9	— 64.2	18	36	50.	Good.
23	b	6	10	— 62.5	18	36	50.	Good.
23	c	0	5	—100.	18	36	50.	Good.
23	d	0	4	—100.	18	36	50.	Good.
24	a	3	15	— 83.3	27	54	50.	Good.
24	b	3	14	— 82.3	27	54	50.	Good.
24	c	2	19	— 90.5	27	54	50.	Good.
24	d	4	19	— 82.6	27	54	50.	Good.
24	e	3	14	— 82.3	27	54	50.	Good.
25	a	7	17	— 70.8	21	44	48.8	Good.
25	b	4	14	— 77.7	21	44	48.8	Good.
25	c	0	12	—100.	21	44	48.8	Dry.
26	. . .	3	15	— 83.3	?	?	45.	Good.
27	a	0	14	—100.	32	71	45.	Good.
27	b	1	5	— 83.3	32	71	45.	Good.

cents. The table includes those animals which were fairly active in response but does not give individuals obviously unable to respond because of a lack of slime secretion. The positively geotactic animals, with two exceptions, are all found in the upper half of the table and almost all the negative animals in the lower half. Supposing other conditions the same, we can say that those animals in which the ratio of anterior to posterior regions is as 2 : 3, or greater, will be positively geotactic. Those between the ratios of 2 : 3 and 3 : 5 will be more uncertain in their geotaxis, which will depend largely on the combination of other conditions. Finally, those in which the ratio is less than 3 : 5 will almost invariably be negatively geotactic. The nearer one gets to the extremes, the greater the accuracy of prediction. This prediction, it is understood, applies only to animals tested on the glass plate.

An examination of the ninth column shows that the few cases of negative geotaxis occurring in the positive half of the table are probably due to a deficiency in the second most important factor affecting the geotaxis; namely, the condition of the slime secretion of the animal. This secretion may be deficient either (1) in quantity, as in the case of slug 2 b; or (2) in quality, as was the case with slug 10. Of the two cases of positive geotaxis occurring in the negative half of the table, the first, that of slug 18, is easily explained as due to an extraordinary tenacity of the mucus. Moreover in this, and more markedly in the case of slug 22 b, the slugs were very large and rather slow in their movements. Slug 22 b, instead of moving ahead actively, like most slugs when in good condition, often swung its head toward the earth without any forward movement, and hence did not give the pull of gravity the most favorable opportunity to work on the posterior region of its body. This connects itself with a general observation on all the animals. When active, they are usually very precise and uniform in their responses. If stupid, slow, and averse to movement, — a condition in which the best of them sometimes get, — they will either obstinately refuse to move, or else, keeping the posterior region firmly fixed, will swing the head end toward the earth. Sometimes such a slug will slowly move in a circle, first down then up, and finally curl itself up, like a dog by the fireplace, and apparently go to sleep. This peculiarity may be connected with the food conditions of the animals, as will be shown in a set of experiments to be given later on.

The two most important factors in determining the geotaxis of individual slugs are, therefore: first, the proportion of the anterior (mantle-covered) and posterior (uncovered) regions of the body; secondly, the

character of the slime secretion of the animal. If accurate measurements were made of the two regions of the body, we might obtain exactly the relative weights of these two factors. By means of a spring balance, the effectiveness of the mucus in counteracting gravity could be ascertained with a fair degree of accuracy. A large number of such observations in connection with geotactic tests might, finally, enable us to state precisely what combination of the two factors — weight of regions and strength of mucus — would be necessary to make an animal positively or negatively geotactic. I have made no such calculations, and it would perhaps not be worth the trouble. The suggestion is instructive, however, as indicating the possibilities of predicting, with a certain degree of exactness, a phenomenon which seems at first sight to be entirely haphazard. Perhaps perfect mathematical exactness would, however, never be possible in this case, for, as I shall show a little later, other factors of importance probably enter in to modify the results. However, these too are not out of the reach of precise definition.

Certain slugs are negatively geotactic because gravity pulls the posterior region of the body down faster than it does the anterior region. Since in all slugs the posterior region somewhat exceeds in length the anterior, we should expect all animals to respond in the same way, provided gravity acted in only a mechanical way. But about the same number of slugs go down as go up. Therefore, there must be some other factor, such as an inherent tendency, impelling these positive slugs to seek the earth. But if so, is it not probable that *all* slugs have this inherent tendency to move towards the earth, the tendency being obscured in the negative slug by the superior force of the mechanical difficulties to be overcome? The fact that positive slugs, when deficient in means of resisting the pull of gravity, — that is, when dry, — assume a negative geotaxis, shows that the inherent tendency is sometimes obscured. If this hypothesis is true, then we ought to be able, by diminishing the force of gravity, or better, by increasing the animal's powers of resisting the disproportionate pull on the posterior region, to make the negative animals become positive. Similarly, if this mechanical difficulty of adhesion is the cause of negative geotaxis, we ought, by increasing it, to be able to compel positive animals to become negative. The first end may be attained by substituting for the glass plate a wooden one, which will presumably offer the animal a better chance of adhesion. The second end may be reached by substituting for the glass plate one which has been coated with vaseline or

a similar substance. Both ends may also be attained, to a certain extent, by increasing or decreasing the angle of inclination of the plate. An examination of the tables given by Davenport and Perkins ('97, p. 103) shows that the largest average number of negative responses occurred when the glass plate was vertical; that is, when the mechanical difficulties were greatest. There is a gradual decrease in this average (and a corresponding increase in the average number of positive responses), as the angles of inclination of the plate with the horizon were diminished from 90° to 60° , 45° , and 30° successively. At the still smaller inclinations of $22\frac{1}{2}^\circ$, 15° , 7° , and 0° (i.e., horizontal), however, there is on the whole an *increase* in the average number of negative responses, though this is quite irregular. Since the proportion of anterior to posterior region of the animals experimented on is not known, we cannot tell how far this factor may have been the cause of this irregularity in the sense of the response.

I have made a few experiments by varying for the same individual the angle of inclination of the plate. The animals were all in good condition throughout the experiments. The results — given in Table V. — show a decided increase in negative geotaxis with increase in the angle of inclination.

TABLE V.
PER CENT OF GEOTAXIS AT DIFFERENT ANGLES OF INCLINATION OF THE
SUPPORT.

Animal No.	Angle of Inclination.	Number of Trials.		% Geotaxis.	Condition of Animal.
		+	-		
1	45°	8	2	+ 80.	Good.
1	90°	0	14	-100.	Good.
2	45°	7	1	+ 87.5	Good.
2	70°	8	3	+ 72.7	Good.
3	45°	2	8	- 80.	Good.
3	90°	0	10	-100.	Good.

The most striking case is the complete reversal of geotaxis, seen in the first animal experimented on.

Still more conclusive results were obtained by the substitution of wood or vaselined glass surfaces for the clean glass plate. In order to make sure that the animal's power to hold on varied with different surfaces, and to determine approximately the relative strength of the adhesion, Dr. Davenport suggested the use of a delicate spring balance, such as are used in weighing letters. The animal was placed on a horizontal glass plate. When it had oriented itself, and was moving forward, the pan of a letter balance was held against the side of the animal and gradually increased pressure exerted until the animal was made to slip along the plate. The maximum reading (in ounces) on the indicator was noted. Then the same animal was placed on a wooden plate and a similar test made under like conditions of movement and activity. The same was done on the vaselined plate. A number of such tests were made on each individual. In order to avoid possible differences in results due to a gradual deterioration in the condition of the animal, the sequence of the surfaces was varied in the successive sets (three) of trials so that each surface was once employed for the first experiment of a set. This method proved fairly satisfactory and gave in some instances very striking results.

TABLE VI.

AMOUNT OF PRESSURE REQUIRED TO DISLodge THE SLUG FROM DIFFERENT HORIZONTAL SURFACES.

Animal No.	Wood.	Glass.	Vaselined Glass.
1	1.8 ounces	1.5 ounces	.23 ounces
2	1.25 ounces	.67 ounces	.34 ounces
3	3.16 ounces	2.16 ounces	1.55 ounces
4	4.33 ounces	2.55 ounces	1.55 ounces
5	3. ounces	1.16 ounces	.50 ounces
6	5.7 ounces	3.50 ounces	1.52 ounces

The results recorded for each individual are the averages of three trials on each of the surfaces used. The table shows a considerable difference in the degree of adhesion to the different surfaces. In the last four cases the animals were all very large. They were in excellent condition, having just been captured, and secreted a sticky slime in large quantities.

After being on the vaselined surface, there was a noticeable decrease in the power to hold on to the glass or wood, due probably to the vaseline which still adhered to the animal. Regarding these cases as typical of all slugs, we can say that the wooden surface affords a condition nearly twice as favorable as that of the glass plate for the exhibition of an internal tendency. The vaselined surface, on the contrary, is only about half as favorable as the glass plate; that is, it doubles the obstacles. As a general rule, owing to the irregularities of other influences, the difference between the different surfaces would be, probably, somewhat less. For active, well-conditioned animals, however, we have no hesitation in concluding that the ratios obtained from these cases are fairly representative.

Having thus established the fact that the character of the surface does modify the animal's power to attach itself, I next give a table (VII.) showing the results of a series of experiments on twelve different individ-

TABLE VII.
GEOTAXIS OF THE SLUG ON DIFFERENT SURFACES.

Animal No.	Ratio of Anterior to Posterior Parts in %	Plate at Inclination of 45°.								
		Wooden Plate.			Glass Plate.			Vaselined Glass Plate.		
		No. of Trials.		% Geotaxis.	No. of Trials.		% Geotaxis.	No. of Trials.		% Geotaxis.
		+	-		+	-		+	-	
1	61.	9	8	+ 53.	0	5	-100.	0	5	-100.
2	?	5	0	+100.	6	5	+ 54.5	0	9	-100.
3	52.	5	0	+100.	1	3	- 75.	0	5	-100.
4	47.	7	0	+100.	1	8	- 88.8	0	slips	0
5	76.	5	2	+ 71.4	5	1	+ 83.3	1	3	- 75.
6	50.	7	3	+ 70.	2	8	- 80.	0	slips	0
7	66.6	9	1	+ 90.	1	9	- 90.	0	slips	0
8	83.3	5	0	+100.	10	0	+100.	4	6	- 60.
9	56.	9	1	+ 90.	0	10	-100.	0	0	0
10	61.	5	1	+ 83.3	5	1	+ 83.3	1	5	- 83.3
11	53.	8	0	+100.	1	5	- 83.3	0	slips	0
12	53.5	6	0	+100.	7	2	+ 77.7	2	slips	0

uals. The geotaxis of each animal was tested on three different surfaces, — the glass plate, a circular wooden plate, and a glass plate coated with vaseline. Care was taken to have other conditions as nearly as possible the same. Circular plates were employed so that the animal could be rotated into a horizontal position without being touched by the hand. In several cases a series was made on an animal using the glass surface; the animal was then transferred to a wooden plate and the same number of trials made; the same individual was then put back on the glass plate and as many more tests were made; finally, it was returned to the wooden plate and an equal number of observations made. The same thing was tried alternating between glass and vaselined surfaces.

The second column shows what per cent of the length of the posterior region of the animal's body its anterior region is, as previously defined. A comparison of the columns "% Geotaxis" under the different conditions at once shows, in nearly every case, a marked difference in the geotactic response with the three kinds of surfaces. The same number of trials was not always made on a given animal under the different conditions, so that the comparisons are not always on exactly the same basis. The results, however, prove pretty conclusively that all animals have an inherent tendency to move toward the earth. On the glass plate, the animals moving upward and downward are about equal in number, the reasons for which we have already given. On the wooden plate, which affords the best of the three surfaces for adhesion, all the animals have become positive. A vaselined surface offers still greater difficulties to positively geotactic responses; it compels the positively geotactic animals to become negative (Nos. 2, 5, 8, 10). Some animals are utterly unable to adjust themselves to this extraordinary condition, especially if not endowed with the power of secreting excellent mucus. These animals either vainly cling with the anterior end of the body to the plate, while the posterior region slips downward, thus directing the animal up, or they roll off the plate altogether as soon as it is placed in an inclined position. For this reason some of the animals negatively geotactic on the glass plate gave no geotactic response when they were placed on the vaselined surface. These facts, then, conclusively answer in the affirmative our second question. All slugs have a tendency to move toward the earth.

Now the question naturally comes up, Can we not assist this tendency in those animals which are negatively geotactic on a glass surface by bringing some other stimulus — light, for example — to bear upon them? This slug is negatively phototactic to strong light, as the third part of this investigation will show. By exposing the animals to strong light, can

we not make the desire for darkness coöperate with the inherent positive geotactic tendency to such an extent that the two together will overcome all mechanical difficulties and cause the animal to move downward? The following table (VIII.) answers this question in the affirmative.

TABLE VIII.

GEOTAXIS OF SLUG ON GLASS PLATE AT AN ANGLE OF 45° INFLUENCED (1) BY GRAVITY ALONE, AND (2) BY GRAVITY AND STRONG LIGHT.

Animal No.	Size.	Gravity alone.			Gravity + Influence of Strong Light.		
		No. of Trials.		% Geotaxis.	No. of Trials.		% Geotaxis.
		+	-		+	-	
1	Big	0	17	-100.	8	8	+ 50.
2	Big	0	14	-100.	7	5	+ 58.3
3	Big	1	7	- 87.5	2	2	\pm 50.
4	Big	0	5	-100.	2	4	+ 66.6
5	Medium	3	9	- 75.	4	4	\pm 50.
6	Small	0	5	-100.	0	5	-100.

These experiments were carried on in the evening. The animal was first tested on a glass plate at an angle of 45° in the dark, in the ordinary way. Then it was placed on a horizontal glass plate and strong lamp light thrown directly upon it for a few seconds. In most cases it immediately gave a negative response to the light. When definitely oriented, the plate was again placed in the box at an angle of 45° and the box covered with a black cloth. Two or three geotactic observations were then taken, and the animal again exposed to strong light. The exposure to light was repeated about three times in the course of ten observations. The table shows that the influence of light has been to change a condition of strong negative geotaxis to one of indifference. The only exception is No. 6, which seemed little affected by the light. I hope to make a fuller study of the combined action of light and gravity later.

It has been said that all slugs have an innate tendency to move toward the earth. Now, this tendency is probably due to the environment and habits of the animal. The slug, we know, is nocturnal in its habits. In the nighttime, it is actively moving about in search of food. In the daytime, it is inactive and seeks concealment, which is of course accom-

plished by moving toward the earth. In hunting for food, it must naturally do some climbing. These facts lead us to expect a possible difference between the geotactic response of the nighttime and that of the daytime. My experiments in this matter, however, gave inconclusive results. But the animals experimented on were not in their normal environment. There was no light and little change in temperature to assist the instinct, if it exists, in divining night from day. Moreover they did not have to seek food, for it was constantly supplied them. Such being the case, the instinct of concealment would be the main environmental influence on the animal, and this impels it toward the earth.

These experiments have shown, then, that when the mechanical conditions are favorable, most animals exhibit a positive geotaxis. This is as we should expect. There were, however, a few exceptions. A few animals went up when all the factors enumerated seemed to point to the probability of a downward movement, and there were also a few animals which went down when the mechanical difficulties were such as should have impelled them upward. As previously noted, the upward-moving animals sometimes displayed an unusual amount of activity, and the exceptional cases of positive geotaxis in the negative group were those of animals usually slow and stupid. As the effort was constantly made to select only fairly active animals in good condition for producing mucus, there were not many of these exceptions. Knowing the habits of the animal, we may naturally associate its activity with its food condition.

The question then comes up, Does the state of the animal's nutrition affect its tendency to move toward the earth? Does a poorly nourished animal respond to the stimulus of gravity differently from a well-nourished individual? To get an answer to this question, four animals were put into a small box which contained nothing but moist earth. The slugs were kept there for three days, and a series of geotactic tests was then made upon them. Two of the four individuals were inactive, and so unsatisfactory in response that no series was obtained. The other two were rather restless, but precise in response. All the animals were then returned to the box and supplied with fresh cabbage leaves. The next morning another series of geotactic stimuli was given. The rather meagre results given in Table IX. are perhaps not worth very much, since only one individual (No. 1) out of the four responded well in both cases.

The ratios given in the second column (Table IX) indicate that slugs Nos. 1 and 2 belong with those of the positive half of Col. 8, Table IV. I unfortunately neglected to control these experiments by observing the geotaxis *before* the animals were deprived of food. In

TABLE IX.

COMPARISON OF RESPONSES OF INDIVIDUALS WHEN POORLY NOURISHED AND WHEN WELL NOURISHED.

Animal No.	Proportionate Ratio of Anterior to Posterior Region.	Poorly nourished.			Well nourished.		
		No. of Trials.		% Geotaxis.	No. of Trials.		% Geotaxis.
		+	-		+	-	
1	70.	3	9	-75.	7	2	+77.7
2	60.	1	8	-88.8	4	1	+80.
3	56.	0	0	0	12	6	+66.6

both instances (Nos. 1 and 2) the animals were rather dry, and they were not noticeably different in this respect after being well fed. No. 2 was less active and less precise in response after it had had plenty of food. I think these experiments too few to warrant laying much stress upon them, but I have given them here because they at least point in the direction of what we might reasonably expect, since the natural desire of the animal to escape from its narrow prison and the impulse to seek food would both tend to make it go up, if given the opportunity.

Another element which may alter the slug's inherent geotaxis is probably the state of fear. This element may be combined with the impulse to seek food, as is perhaps the case in the instances just given, or it may operate by itself. Animals which had just been captured were always kept in a small tin box. The captured animals would thrust themselves between the box and lid, which was not perfectly tight, in their endeavors to escape, and they had to be frequently pushed back. When they were transferred to the large box mentioned at page 187, it was always found that they had all collected in the upper part of the smaller box. This may have been solely for the purpose of getting air, but such animals put on a glass plate were exceedingly active and restless, and usually exhibited a decided negative geotaxis. I have not made any careful set of experiments to find out whether these negatively geotactic animals afterwards became positive. In one instance, I confined over night in a small flower-jar a slug (not a freshly captured one) which had shown a very decided positive geotaxis. In the morning it was found at the top of the jar, and, when placed on a glass plate, showed great activity, as though it sought to escape. In every one of the tests which I then made, it responded negatively. From these few observations, it

would seem that fear, by impelling the animal to escape from captivity, may alter its geotactic response. Such freshly captured slugs, moreover, which seem unusually restless and excited, respond more capriciously to the stimulation of light, as some later experiments will show.

SUMMARY OF PART II.

The results of the foregoing experiments warrant the following conclusions: —

1. On an inclined *glass plate*, all slugs give a geotactic response.
2. Certain slugs give a decided positive, others a markedly negative geotactic response; a few are somewhat indifferent.
3. The geotaxis of animals kept in confinement does not vary much on different days, nor at different times on the same day.
4. The occasional vagaries in the responses of individual animals are to some extent due to thigmotactic and phototactic influences.
5. The different geotactic response, on a *glass plate*, of different individuals is due mainly to two factors: (a) The quantity and quality of the slime secreted, which is a very important factor; (b) the relative proportions of the length of the anterior and the posterior regions of the animal's body. All the conditions being the same, it is this factor which "determines whether the head end will be directed up or down."
6. If the ratio of length of anterior to posterior region of body is 2:3, or more, and the mucus is of good quality and sufficient quantity, the slug will be positively geotactic.
7. If the ratio is 3:5, or less, the animal will usually migrate upward, and the nearer the ratio approaches 1:2 the more apt is the slug to respond negatively.
8. In a small number of individuals, in which the ratio lies between 2:3 and 3:5, the response will depend largely on the condition of the mucus and coöperation of other factors.
9. All slugs have a natural tendency to move towards the earth. This tendency is masked in the animals which are negatively geotactic on a *glass plate* by the greater pull of gravity on the disproportionately larger and heavier posterior region of the animal.
10. The general downward tendency may vary normally at different times of the day, owing to the animal's habit of remaining in concealment in the daytime and feeding at night.

III. PHOTOTAXIS.

The influence of light on the direction of locomotion has been very generally noticed among organisms, even the mostly widely separated. The swarm spores of many algae, desmids, and other lowly organized plants, are as truly responsive to light stimuli as are crustaceans or vertebrates. According to the character and direction of the stimulating light rays, two kinds of light responses have been distinguished. Phototaxis is the response with reference to the *direction* of the rays of light. The organism moves in the path of the ray, either positively (toward) or negatively (away from it). The response to different *intensities* of light from which the directive force of the rays has been eliminated is known as photopathy. A photopathic animal is one that selects, out of a series of uniformly increasing intensities of light, a limited field of a certain intensity.

Some animals, like butterflies and fresh-water Entomostraca, are strikingly positively phototactic to diffuse daylight; others, such as the earthworm and the leech, are as pronouncedly negative. The kind of response (positive or negative) may be different in closely allied forms and in different stages of development of the same species. For example, butterflies are attracted by strong sunlight, while moths are repelled by it. The adult house fly is positively phototactic to daylight; its larva, negatively (Loeb, '90, pp. 69-77, 81-83).

The phototactic sense has been shown in some forms to change with different intensities of light. Thus, Famintzin ('67) found that swarm spores positively phototactic to a certain intensity of light became negative to a light of greater intensity. The same phenomenon has been found true of various flagellates, desmids, diatoms, oscillariae, etc. Wilson ('91, p. 414) found that *Hydra fusca* was attracted by diffuse daylight and repelled by strong sunlight. Finally, the moth's liking for candlelight and aversion to daylight is well known. The fact that many organisms are photopathic — that is, have a preference for light of a certain intensity — makes it probable, in connection with these observed variations in phototactic responses, that, for most organisms, there is an optimum intensity to which they will respond positively. This optimum will vary widely in different species, probably according to the habits and the usual environment of the species. Inhabitants of sunny pools or the open air will have an optimum of relatively high intensity; those which dwell in the ground or in shady places

will have a correspondingly lower optimum. May it not be that every organism will respond positively to a certain range of light intensities and negatively to another range of intensities which is greater? The nature of the phototaxis may sometimes be gradually changed by organisms becoming acclimated to new conditions. Verworn ('89, pp. 47-49) found that a culture of the diatom *Navicula brevis*, which ordinarily is negatively phototactic to very weak light, became positively phototactic when reared for several weeks near a window. Groom und Loeb ('90, pp. 166-167) found that young Nauplius larvae of *Balanus* which were at first positively phototactic to daylight became negatively phototactic later in the day, probably as the result of the accumulated effects of this exposure.

The character of the light responses, as was the case with geotaxis, depends also to a certain extent on other external conditions, such as those of temperature, the states of density and pressure, and various chemical influences. *Polygordius* larvae, when gradually cooled from 16.5° C. to 6° C., were found by Loeb ('93, pp. 90-96), to change from a negative to a positive phototaxis. Like results were obtained by him from Copepoda. When the temperature was raised from 6° C. to 16° C., the animals again became negative. Increasing the density of sea-water by the addition of sodium chloride produced a change from a negative to a positive response, thus acting like diminished temperature. Engelmann ('82, pp. 391-392) showed the apparent phototactic response of chlorophyllaceous ciliates to be really a chemotactic attraction for oxygen, which chlorophyll can produce only in the light. These facts make it important in any study of light response to consider other possible influences, and above all to take account of the strength of the stimuli used.

Davenport and Perkins ('97) found that the slug (*Limax maximus*) responded with marked precision to the varying stimuli of gravity at different angles of inclination of the glass plate. The precision of response varied correlatively with the force of gravity. In fact, the parallelism was almost perfect. The question naturally rises, Is there a similar parallelism between other stimuli and their responses?

A very little experimentation shows that the slug is extremely sensitive to light. We have already seen how light may enter in to modify the action of gravity. Casual observation shows that the response is in most cases negative, — the animal moves away from the source of light. Owing to its method of locomotion, the slug is easily experimented on. It moves slowly and deliberately. In regard to its responses to light, the following questions suggest themselves: (1) Are all individuals negatively phototactic to artificial light? (2) Does the precision

of response vary correlatively with the intensity? (3) Within what limits of intensity is the animal responsive? (4) Does the kind of response vary at different intensities? (5) Is there a difference in the sensitiveness to light of the two sides of the animal's body? (6) In what part, or parts, of the animal's body does the sensitiveness reside? (7) How does the animal move when in the dark and deprived of all stimulating influences? These various problems came up gradually as the work progressed and were considered in turn. Other interesting studies have suggested themselves in the course of the investigation, but there has not been time to go much beyond a consideration of the questions above proposed. The experiments performed were all phototactic; that is, they were studies of the response of the slug to the direct rays of light.

Methods. — The methods used were simple. For light, the standard candle and the ordinary small Christmas candle, of a one fourth candle power, were employed. The candle was placed in a box 50 cm. (20 inches) high and having a bottom 12.5 cm. (5 inches) wide and 20 cm. (8 inches) long. It could be raised or lowered to any desired position by means of an adjustable stage inside the box. A circular opening in the middle of one of the broad sides of the box 2 cm. ($\frac{1}{2}$ inches) in diameter permitted the light to pass out. This opening was covered by a piece of oiled paper, so as to give a well-defined uniform source of light. During the experiment the box was closed by a lid. The intensity of the light was varied by altering the distance between the box and the animal. Additional thicknesses of paraffined paper were also employed when it was desired to greatly diminish the intensity of the light. The animal was put on a circular glass plate which rested horizontally on a support, and the box was raised so that the centre of the light opening was in the same horizontal plane as the body of the animal. The movement of the slug from its original position was measured in degrees in the following manner. A circle of the same size as the glass plate was described on a sheet of thin paper and divided by radii into 72 sectors of 5° each. This sheet was pasted to the under side of a second circular glass plate (of the same size as the first), on which also a heavy base line was drawn, corresponding with a diameter of the circle. This second plate was so placed that the centre of the source of light was on a line perpendicular to the base line at its middle point. The slug was put on the first glass plate, which could be rotated so as to bring the animal into any desired position with reference to the base line. The experiments were carried on in a dark room provided at one end with a hinged window which could be easily

and quickly thrown open. The window was covered with a thick, black cloth, so that, when closed, external light was almost completely shut off. Unfortunately, it was impossible, owing to the position and nature of the room used, entirely to equalize all conditions. The temperature was not the same from day to day and varied somewhat in different parts of the room. Generally, it was so hot and close that it was necessary to leave an opening between the sashes, and this of course created a slight draft and produced irregularities of temperature. No account was taken of the varying humidity of the atmosphere, a factor which may have somewhat influenced the animal's locomotion. Moreover, as the room was not perfectly light-tight, there were feeble light stimuli in addition to the artificial ones used. However, all these imperfections were but slight, and, since they entered more or less into all the experiments, could not greatly alter the relation between the results, which was the main thing sought in the investigation. Other unestimated possible influences were the nutrition of the animal and such slight thigmotactic stimuli as could not well be avoided.

The strength of the different intensities of light used was measured by moving a piece of paper, the centre of which was oiled, between a light of known intensity and the light whose intensity it was desired to know, until the oiled spot on the paper was not distinguishable from the rest of the paper. The distance from this point to each source of light was then measured. Since the intensity varies inversely as the square of the distances, it is an easy matter to calculate the relative strengths. This method is accurate enough for all ordinary purposes.

Operations and Results. — In beginning any experiment, the slug, as soon as it had definitely oriented itself, was rotated into such a position that the axis of its body coincided with the base line, and its head was at the centre of the disk. The window was then immediately closed and the time noted. At the expiration of 45 seconds, the window was thrown open and the animal's position instantly noted. The extent of positive or negative migration was at first ascertained by finding the length of the arc stretching from the base line to the radius which was *parallel with the axis of the slug's body*. Any movement into the half of the circle toward the source of light was called positive; any movement into the other half, negative. It would occasionally happen that an animal would at first move into the positive half of the circle and then turn away from the light. In this case the axis of orientation made a negative angle with the base line, although the animal itself lay in the positive half of the circle. Later, in the course of the experiments, the positive or

negative movement of the animal was measured by taking the radius which passed *midway between the two tentacles*, without regard to the position of the body axis. A comparison of the two methods showed but little difference in the results. The animals only occasionally made these irregular responses, first in a plus and then a minus direction. As a rule, the migration was unequivocal after the head end had oriented itself to the stimulus. Experiments were made with 18 different intensities of light, each constituting a "series." Six successive observations were made on each individual (3 with the right side exposed; 3 with the left), and from 8 to 14 animals were employed in each "series." *i. e.*, at each intensity of light, making a total of from 48 to 84 observations at each candle power used. A summary of the results for each of 18 such "series" is given in Table X.

The first column gives the number of the series; the second, the intensities of light. This intensity is expressed in terms of the standard candle power at a distance of one meter. The next column (3) shows the total positive migration of the (8 to 14) animals experimented with. Column 4 similarly gives the total negative migration. Column 5 represents the average arithmetical angular deviation from the original position due to phototactic stimuli, effected in a period of 45 seconds by all the slugs, without regard to the positive or negative character of the individual phototaxis. This average was obtained by adding together the average phototactic responses (whether plus or minus) of each *individual* of the series and dividing the result by the number of animals. The average plus or minus phototactic response (algebraic average) for each series (column 6) was obtained by getting the difference between the sums of all the plus and all the minus movements of each *series* and dividing this difference by the number of tests (observations) made. Column 7 gives the number of positively phototactic animals in each series; column 8, the number of negative animals; column 9, the number of indifferent animals; and column 10, the total number of individuals employed in each series. The sequence of the series is not the same as that of the experiments, but is based on gradually diminishing light intensities. I did not determine the possible influence of the heat of the candle for each of the series, but in one series of experiments in the dark (18*b*), a candle, covered (to shut out the light) with an opaque paper of the same thickness as the paraffined paper, was left burning at a distance of 30 cm. (intensity .676 C. P.).

A casual glance at the table at once answers the first of the questions proposed in the statement of the problems (pp. 207-208). All slugs are

not negatively phototactic. At the strongest intensity of light used, two animals exhibited a positive phototaxis, — they moved toward the stimu-

TABLE X.
RESPONSES OF THE SLUG TO LIGHT.

1	2	3	4	5	6	7	8	9	10
No. of Series.	Intensity of Light.	Total Phototactic Migration in Degrees.		Average Response in Degrees in a Period of 45 Minutes.		No. of Animals.			
		+	—	Arithmetical Sum.	Algebraic Sum.	+	—	0	Total.
1	.676	330	2155	45.5	—38.	2	6	0	8
2	.382	625	2772	40.	—25.5	2	12	0	14
3	.169	440	2430	27.5	—25.5	2	11	0	13
4	.042,4	625	1330	26.	—11.7	2	8	0	10
5	.010,5	250	1165	17.6	—15.	2	8	0	10
6	.004,7	830	1140	16.1	— 5.1	2	7	0	10
7	.001,69	405	760	9.1	— 6.	3	6	1	10
8	.000,754	695	595	13.	+ 1.4	7	5	0	12
9	.000,424	1145	895	17.	+ 3.5	6	4	2	12
10	.000,260	823	345	14.5	+ 7.9	7	3	0	10
7a	.001,69	365	480	4.6	+ 1.7	4	7	0	11
8a	.000,754	845	345	11.8	+ 8.3	7	3	0	10
9a	.000,424	985	130	14.7	+14.2	9	1	0	10
10a	.000,260	740	435	11.	+ 4.2	8	4	0	12
11	.000,022	1395	55	22.3	+22.3	10	0	0	10
12	.000,009,6	630	515	8.6	+ 2.	7	3	0	10
13	.000,003,35	865	255	13.	+10.	8	2	0	10
14	.000,002,00	800	170	10.5	+10.5	9	0	1	10
15	.000,001,26	850	415	11.1	+ 7.2	7	3	0	10
16	.000,000,185	1375	145	24.	+20.5	7	3	0	10
17	.000,000,018,8	445	370	8.9	+ 1.	6	4	0	10
18a	Darkness.	1440	1290	3.6	+ 1.2	10	8	2	20
18b	" with candle heat.	475	635	8.7	— 3.	3	6	0	10

lating light rays. Here, then, arises another problem, similar to the one treated of in the first part of this paper, viz., What determines whether a particular slug shall be positively or negatively phototactic? In the first series of experiments — in fact throughout this whole set — the animals used were about equally divided between large, small, and medium-sized individuals. The two positive animals in series 1 were both of large size. They were very active. The only peculiarity wherein they seemed to differ from other individuals was in the unusually sticky character of the slime. Whether there is any correlation between this fact and the liking for strong light, I am not prepared to say. It is possible — and certain observations seem to indicate that it is highly probable — that the food conditions of the animals have some influence on their responses to light, as they were shown to have on their responses to gravity. The psychic state of the animal is also to some extent, I think, a factor. Freshly caught slugs when put on a glass plate sometimes acted as if in great fear. They displayed unusual activity and were very erratic in their movements. If forcibly checked or held, they made strenuous efforts to escape. The great activity of the positive individuals indicates a possible state of fear. One animal in particular seemed highly abnormal. Several times it moved directly toward the circular field of light and even placed its tentacles against the oiled paper which covered the opening. This was the only individual in the whole course of the experiments which exhibited a response like that of moths. No definite set of experiments was planned or carried out in regard to this matter.

As we run down column 5, we see that the average arithmetical response varies quite strikingly at the different intensities. The first seven series show a gradual decrease in the average response as the strength of the light is diminished. Although not so regular, there is also a gradual decrease in the degree of negative response on the part of these seven groups of animals, as shown by the average algebraic sums of their responses (column 6).

Owing to the constant dying off and deterioration of the stock, it was found impossible to use the same set of animals in all the different series of experiments. Moreover, this was not desirable, for the reason that an animal which is constantly experimented on gradually loses its sensitiveness, and thus its responses become untrustworthy. Not knowing the factors which determine the kind of phototaxis, it was of course impossible to make a uniform selection in this respect. We see, however, that the number of negative animals (column 8) is less at the

weaker intensities than at the stronger. When we come to series 8 of the table, we meet with a new condition of affairs. Instead of a still further decrease in the amount of deviation, there is a sudden slight increase, from 9.1° to 13° , and a reversal in phototaxis for the series from an average response of -6° to $+1.4^{\circ}$. The number of positive individuals has increased from 3 to 7. It was because of this striking change that it was thought best to repeat this series and the three succeeding ones on another set of animals. The absolute positive or negative migration was this time taken without regard to the position of the body axis. Series 7a, 8a, 9a, and 10a are hence taken at the same intensities as 7, 8, 9, and 10 respectively. These repeated series indicate as strongly as the first set that an intensity of .001,69 C. P. very nearly marks the lower limit of negative phototaxis in the slug. Somewhere near a candle power of .000,754, lies an intensity which attracts about as many animals as it repels and in about the same degree. That is, the average phototaxis (algebraic sum) is zero. Below this intensity, there is more attraction than repulsion, and hence there is an average increase of migration toward the light. The table shows that the average positive response increases to some extent correlatively with the diminution of the light intensity, up to a certain point. This point, according to the results here obtained, is the intensity of .000,022 C. P., where the average movement toward the light, in a period of 45 seconds, was through an angle of 22.3° . As we go below this intensity, there is again a falling off in the strength of the positive response, which diminishes, however, with a good deal of irregularity until absolute darkness is reached. These facts will become more apparent from the study of their graphic portrayal in the curve here given.

The continuous line represents the curve as plotted from the results of Table X., column 6; the dotted line, the curve of responses as one may assume theoretically it would have been, could all of the conditions other than intensity of light have been equalized. The abscissae here represent the logarithms of the intensities of light + 10. Beginning with darkness on the left end, there is a constant increase of intensity as we move toward the right. The sines of the angles of response are marked off on the ordinates. Remembering that the left represents a region of weak intensity and the right a region of strong light, that all points above the line $x\ x'$ are points of positive response and all points below it of negative response, we can understand the significance of the curve. In the region of strong light, the curve lies far below the line $x\ x'$, but gradually rises toward and finally crosses it, as the light

CURVE OF RESPONSES TO LIGHT.

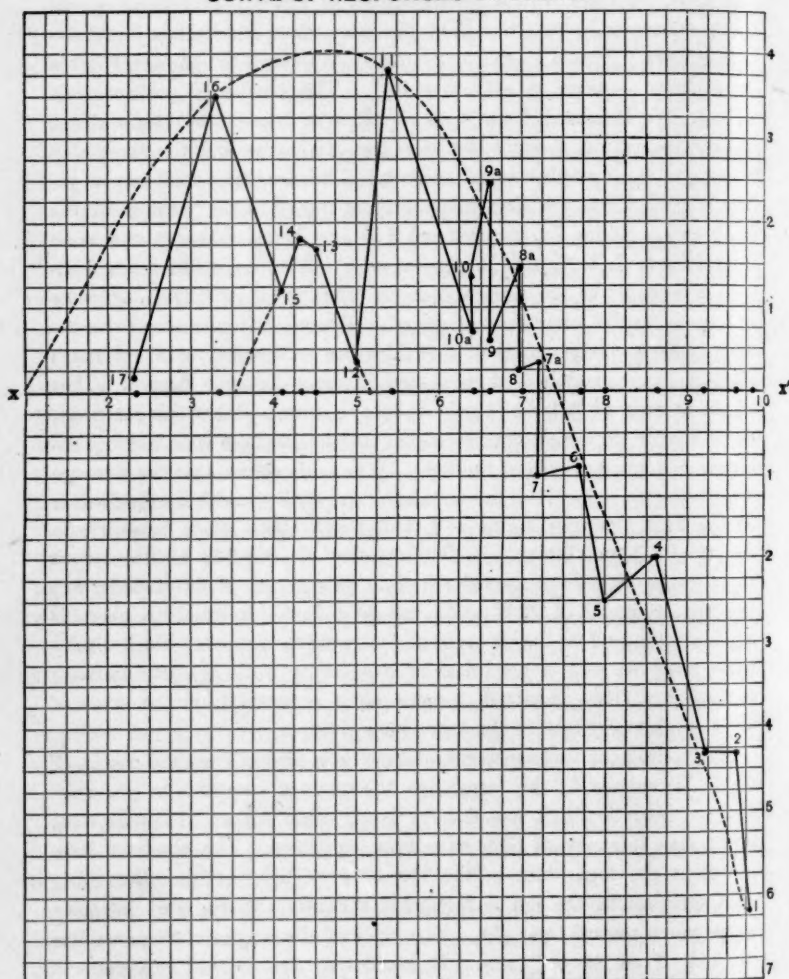


FIGURE 2.

Curve of Responses to Light. *Abcissae* are logarithms of light intensities plus 10; *ordinates* are sines of angles of responses multiplied by 10.

diminishes in strength. Then there is a gradual increase in positive reaction, which reaches its height in a response of $+22.3$ at a .000,022 C. P., and then falls toward the zero line as we approach darkness. There is some irregularity in the negative region, but on the whole the rise is gradual. In the region of positive response, there is a considerable lack of regularity, especially marked by the interpolation of one series (12) of very low response between the two series of greatest response. These series intermediate between Nos. 11 and 16 represent later experiments than the two series bearing those numbers. Having obtained such a marked positive response at two widely separated intensities of light, it was thought desirable to get other intermediate series. Hence, the order of the series as arranged in the table, on the basis of gradually diminishing light intensities, does not, as already stated, represent the order in which the series were obtained in my experiments. While the slugs, thus far, had, on the whole, been in good active condition, they were not so in these intermediate series. Although a fresh supply was obtained, all the animals seemed much more stupid and irresponsive than usual. Some of them refused to move, when put on a plate, and many of those that did, responded in a very half-hearted way. The cause of this unusual lack of activity, I could not discover. It may be that a slight change in the food of the animals, which I made at this time, was partly responsible. At any rate, instead of obtaining responses intermediate in amount between those of series 11 and 16 as might have been expected, the results were as have been given. Series 12 was the last one taken. In this, the animals were noticeably more stupid and irresponsive than in any of the preceding experiments. It is very evident from these results, I think, that the precision of response will vary to some slight extent from day to day. The negative responses — those to strong intensities of light — will not be as variable at different times as the positive responses — those to weaker stimuli — as the curve shows. The varying thermal conditions of the room, already mentioned, may have been in part a cause of this irregularity. Furthermore, an animal that has had plenty of food is likely to be stupid and slow in movement and is more apt than a hungry one to seek darkness and concealment. On the other hand, a hungry, active slug will probably exhibit positive phototaxis in a most marked and sometimes abnormal degree, as was the case occasionally with the positive animals at the strongest light intensities. Besides this individual variation, there is, I think, a general variation for all slugs from time to time, for reasons imperfectly known, which will find its expression in curves of different heights.

Thus the less responsive animals of the intermediate but later series mentioned fall into a less prominent curve, as is indicated by the shorter dotted line in the diagram. The curve of positive response approaches, but never actually reaches, the zero line. Even in darkness there is a slight positive migration. This series (No. 18a) represents the average of two series of experiments, one of 54 and the other of 66 determinations, each taken at different times during the investigation. This slight positive response — speaking of it as positive with reference to the position of the source of light in the preceding series (17) — may be independent of conditions of light and due to several causes. As mentioned before, the thermal conditions of the room were not uniform, consequently the positive response may have been a response to heat. The movement was away from the window and hence might be explained as a negative response to the repeated inflowing of daylight, when the window was thrown open to make observations. In the last few experiments an opaque screen was put up between the animal and the window. In these cases the average of the responses was slightly negative, so there is some reason to suppose that it was in part the position of the window in the previous experiment that determined the slight positive migration. The actual phototactic responses to the candle light in the positive half of Table X. would then be the observed responses minus this small positive movement in the dark. The actual negative responses to the strong intensities would be the observed responses plus this increment. In series 18b the box was placed at a distance of 30 cm. (C. P. 0.676) with the light burning, but the opening was covered with a piece of black paper to shut out the influence of the light while leaving that of heat. The small average response of -3.0 may possibly be regarded as a thermotactic one, and, if so, will have to be deducted from the negatively phototactic response to this intensity of light. For intensities less than the 0.676 C. P., the response to the heat would be correspondingly less.

We can now answer the second and fourth questions (pp. 207–208) by saying, — that the precision of the phototactic response does, on the whole, vary correlatively with the intensity of the light, and that the kind of phototaxis (positive or negative) is not the same for different intensities of light. The slug gives a negative phototactic response to strong light, a positive one to weak intensities, and is neutral to an intensity somewhere between the extremes.

A few individuals were tested successively at different light intensities in order to find out with what precision an individual's phototaxis might vary with a change of intensity.

TABLE XI.

RESPONSES OF INDIVIDUALS TO DIFFERENT INTENSITIES OF LIGHT.

Animal No.	Intensity.	Response.	Intensity.	Response.	Intensity.	Response.
1	.382 C. P.	-36.°	.169 C. P.	-34.°	.067 C. P.	-27.°5
2	.382 C. P.	-39.°	.169 C. P.	-14.5°	.067 C. P.	-10.°
3	.382 C. P.	-42.°	.169 C. P.	-31.°	.067 C. P.	-23.°

In all these cases, there is seen to be a gradual diminution in the degree of response as the intensity of light diminishes. Again, from an animal which responded negatively to a certain intensity of light, a positive response could be got by weakening the light sufficiently (Nos. 2 and 3, Table XII.), and a positive animal could be made to give a negative response by using stronger light (No. 1, Table XII.), as the following instances show.

TABLE XII.

RESPONSES OF INDIVIDUALS TO DIFFERENT INTENSITIES OF LIGHT.

No.	Intensity.	Response.	Intensity.	Response.	Intensity.	Response.	Intensity.	Response.
1	.382 C. P.	+41.°	Strong Light	-22.°				
2	.676 C. P.	-15.°	.0424 C. P.	+35.°				
3	.169 C. P.	-37.°	.0188 C. P.	-2.5°	.0067 C. P.	-32.°	.0047 C. P.	+36.°

No. 3, Table XII., shows a less regular response than any of the other animals. From a response of -37° it drops to one of -2.5°, and, under the influence of a still lower intensity of light, it again rises to a marked negative response of -32°. At a still lower intensity, it gives a striking positive response of +36°. Here, however, we have well illustrated in particular individuals the law laid down for all slugs, — that they are negatively phototactic to strong intensities of light, the precision of response varying correlatively with the intensity of the stimulus; that to weak intensities they are positive; and that to a certain intermediate intensity they are neutral.

A glance at the intensity column (Table X.) shows that the slugs are

responsive to a very wide range of intensities. They would probably continue to respond negatively to still stronger light, until the light became strong enough to kill the animal. They respond positively to a light (series 16) less than one three millionth part as intense as the strongest intensity experimented with. The response to the weakest intensity used (series 17) is less than the positive migration in the dark. Hence we cannot speak of this as a phototactic response. This attenuation of light was so weak that I could not be sure I saw it myself, and had constantly to reassure myself by approaching it. The slug is evidently sensitive to a very minute degree of light.

Where does the slug's sensitiveness reside? The first and most natural answer is, that the eyes are the important organs. The matter was tested on five different individuals. The normal phototactic response was first taken with a .676 candle power. Then the dorsal tentacles, bearing the eyes, were snipped off with scissors and the animal again experimented on. The results are given in Table XIII.

TABLE XIII.
EFFECT OF AMPUTATION OF TENTACLES.

Animal No.	Normal Phototactic Response.	Response after Amputation of Dorsal Tentacles.	Ventral Tentacles also Amputated.
1	-70.°	+41.°	+7.°
2	-26.°	- 3.°	
3	-44.°	-29.°	
4	-53.°	+16.°	
5	-65.°	+ 6.°	

As soon as the operation was performed, the stumps were retracted, as the tentacles are when stimulated by touching, or by strong light. After a moment or two, the animal again rolled out the stumps and began moving forward in perfectly normal fashion, as though nothing had happened. The only observable difference was a perhaps slightly increased activity. This table (XIII.) shows a striking effect of the amputation on the phototactic response. In some cases, the animal deviated but very little either positively or negatively from its original position, but kept on moving ahead in a straight line. In other cases, the amputation seemed to cause a change from a strongly negative to a

more or less positive response. In the case of animal No. 3, removal of the eyes did not seem to altogether prevent, though it considerably reduced, the negative response. Thereupon, the ventral tentacles were also amputated and the result then was a slight positive response. Since there is probably some shock to the nervous system by the amputation, these results ought to be corroborated by other experiments where the eyes are covered over with some substance to shut off the rays of light. This, I have not yet succeeded in doing satisfactorily.

The experiment of removing only one of the ocular tentacles was tried on two different animals with the following interesting results.

TABLE XIV.

COMPARISON OF EFFECT OF AMPUTATION OF RIGHT AND LEFT DORSAL TENTACLES.

Animal No.	Normal Phototactic Response.	Response after Amputation of	
		Right Tentacle.	Left Tentacle.
1	-70.°	-27.°	
2	-55.°		+8.°

In the case where the right tentacle was removed, the animal still responded negatively with considerable precision. Amputation of the left tentacle, in the case of No. 2, on the other hand, resulted in a slight positive phototaxis. While these two cases by themselves have little, if any, significance, taken in connection with facts now to be discussed, they seem to indicate a greater degree of sensitiveness to strong light on the part of the left side of the animal's body than the right.

It will be remembered that our thigmotactic experiments pointed to a possible asymmetry in the sensitiveness of the right and left tentacles of the slug. Do we find a similar asymmetry in the responses to light? Table XV. gives the responses of right and left sides respectively for the 18 series. Column 1 gives the number of the series, column 2 the intensities of light, columns 3 and 4 the total angular migrations in a positive and negative direction for the series when the right side was exposed to the light, and the fifth column the algebraic average (positive or negative) phototactic response of the right side. Similarly, the next three columns, 6, 7, and 8, give the responses of the left side. Column 9 represents the total movement of the series in degrees to the right. This result was obtained by adding the total positive responses of the right side (column 3)

TABLE XV.

COMPARISON OF RESPONSES OF RIGHT AND LEFT SIDES TO LIGHT.

1	2	3	4	5	6	7	8	9	10	11
No. of Series.	Intensity of Light.	Responses of Right Side in Degrees.			Responses of Left Side in Degrees.			Total Movement in Degrees to		Total No. of Anl. mals.
		+	-	Average Photo-taxis + or -	+	-	Average Photo-taxis + or -	Right.	Left.	
1	.676	305	770	-19.	25	1385	-57.	1690	795	8
2	.382	250	1056	-19.	375	1716	-32.	1966	1431	14
3	.169	425	595	- 4.3	15	1835	-46.8	2260	610	13
4	.042,4	255	355	- 3.3	370	975	-20.	1230	725	10
5	.010,5	65	730	-22.	185	435	- 8.	500	915	10
6	.004,7	295	805	-17.	535	335	+ 6.7	630	1340	10
7	.001,69	250	500	- 8.3	155	260	- 3.9	510	655	10
8	.000,754	280	330	- 1.4	415	265	+ 4.1	545	745	12
9	.000,424	530	645	- 3.	615	250	-10.	780	1260	12
10	.000,260	435	245	+ 6.3	388	100	+ 9.6	535	633	10
7a	.001,69	250	210	+ 1.2	115	270	- 5.	520	325	11
8a	.000,754	410	165	+ 8.1	435	180	+ 8.5	590	600	10
9a	.000,424	380	75	+10.	605	55	+17.	435	680	10
10a	.000,260	560	230	+ 9.	180	205	- 0.7	765	410	12
11	.000,022	955	0	+31.7	440	55	+12.7	1010	440	10
12	.000,009,6	160	275	- 3.8	470	240	+ 7.6	400	745	10
13	.000,003,35	460	120	+11.7	405	135	+ 9.	595	525	10
14	.000,002,0	410	90	+10.7	390	80	+10.3	490	480	10
15	.000,001,26	395	320	+ 2.5	455	95	+12.	490	775	10
16	.000,000,185	915	40	+29.	460	105	+12.	1020	500	10
17	.000,000,018,8	210	215	- 0.2	235	155	+ 2.6	365	450	10
18a	Darkness	1220	240	+16.	220	1050	-13.8	2270	460	20
18b	" with candle heat	155	495	-10.	320	140	+ 7.	295	815	10
Totals		9570	8506		7808	10321		19891	16314	
" less 18a & 18b		8195	7771		7268	9131		17326	15039	

and the total negative responses of the left side (column 7), — these responses being necessarily right-hand movements. The total movement in degrees to the left (column 10) was likewise obtained by adding the total negative responses of the right side and the positive responses of the left side. Column 11 gives the total number of animals used in each series.

In the region of negative phototaxis, the total positive and negative angular migrations, and the average negative phototaxis of all the series (1-7, inclusive) when the right and left sides respectively were turned toward the light, were as follows.

TABLE XVI.

SUM OF THE RESPONSES OF RIGHT AND LEFT SIDES WHEN PHOTOTAXIS IS NEGATIVE.

Side turned toward Light.	Total Angular Migration.		Average Negative Phototaxis.
	+	—	
Right.	1845.°	4811.°	13.°1
Left.	1660.°	6941.°	23.°4

This shows on the whole a less sensitive right side, or, to put it differently, a more marked negative phototaxis of the left side. How is it when the animals become positively phototactic? Table XVII. gives the average positive response of the right and left sides for series 8 to 18, including series 7a, 8a, 9a, and 10a.

TABLE XVII.

SUM OF RESPONSES OF RIGHT AND LEFT SIDES WHEN PHOTOTAXIS IS POSITIVE.

Side turned toward Light.	Total Angular Migration.		Average Positive Phototaxis.
	+	—	
Right.	6350.°	2960.°	7.°68
Left.	5608.°	2190.°	7.°75

Here an asymmetrical response is less strongly marked. The left side, however, appears on the average to be somewhat more strongly attracted toward the light. The results prove that the asymmetry in response of the right and left sides cannot be wholly due to a tendency to move toward

the right, for, if this were so, we should expect an average positive response of the right side as much greater than that of the left side, as the average negative response of the left is greater than that of the right side, for both these would mean a greater movement to the right. These facts curiously suggest that the right and left sides are attuned to slightly different intensities of light. Is this possibly due to ancestral habits of life in which environment, acting unequally on the two sides, produced this difference?

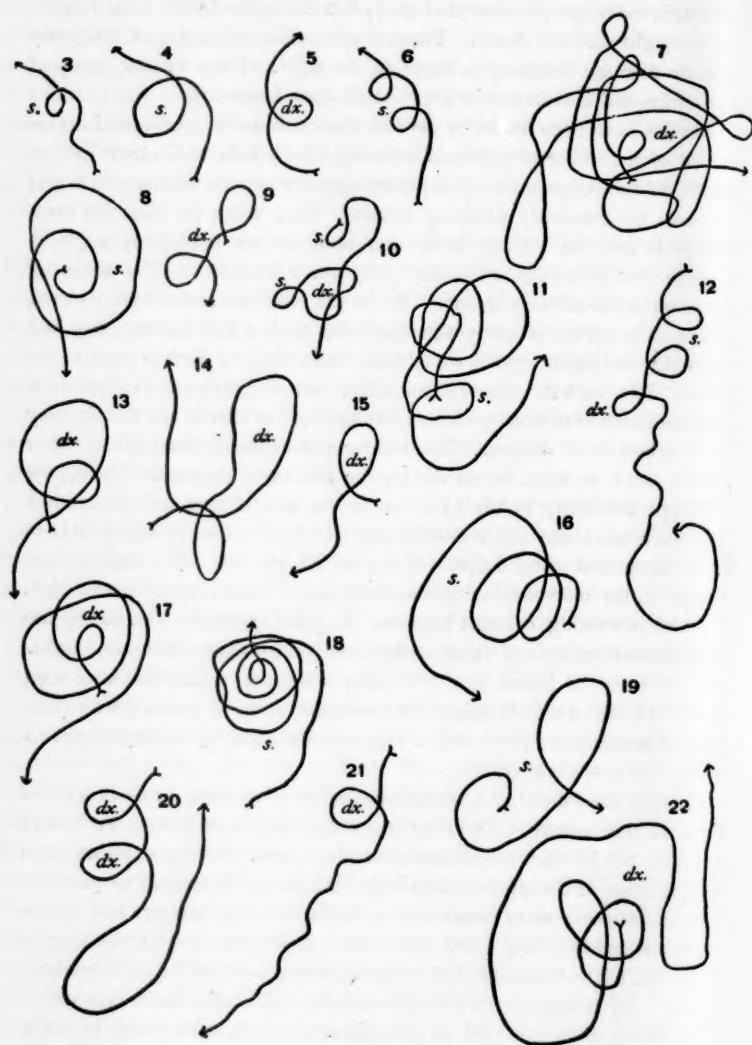
The results obtained for the right and left sides from the experiments in darkness (series 18*a*) are rather puzzling. If the responses are due to some uncontrolled directive stimuli of the kind already suggested, it would seem that the two sides had given opposite responses. As these experiments represent two series taken at different periods, it is the more surprising that they should both show this peculiarity. Again, in the responses to weak candle heat (series 18*b*) the left seems to have been positively, and the right side negatively affected. So far as is known, there was no unequal operation of stimuli on the two sides.

Related to this matter is the question, — Is there any tendency on the part of all slugs to move either to the right or to the left? Individuals were noticed which seemed to have a marked tendency to continue moving toward the right, and there were others which seemed to be as strongly biassed toward the left. Not many seemed entirely indifferent. The total movement of all the slugs in the region of negative response (series 1-8, Table XV.) toward the right side was 8786° (col. 9), and to the left 6471° (col. 10). In the positive region (series 8-18, Table XV.), the total migration toward the right side was 8540° (col. 9), and toward the left 8568° (col. 10). Thus, there seems to have been considerably less migration toward the left in the range of negative responses, but only a slightly greater movement toward the left in the region of positive response. In all the 17 series, there was a migration towards the right of $17,326^{\circ}$, and towards the left of $15,039^{\circ}$. That is, there appears on the whole to have been a slightly greater average movement for all slugs toward the right than there has been toward the left. What do we find to be the case with the animals experimented on in the dark? Out of the 120 determinations made on 20 animals in the dark (series 18*a*), the amount of right-hand movement was 2270° and the left-hand movement only 460° . That is, there was nearly five times more migration toward the right than there was toward the left. In series 18*b*, however, there seems to have been a marked preponderance of movement toward the left. From the foregoing experi-

ments, it seems pretty clear that there is a difference in the sensitiveness of the right and left sides. There is also some indication of a slightly greater average tendency to move to the right. But a further study of the undirected movements of slugs in the dark is needed.

Studies have been made by several observers on the undirected movements of a number of different animals, chiefly ants and other insects. In all animals experimented on, there appears to be a tendency to travel in loops or constantly widening spirals. Man, when he loses his way, travels in a circle. Some interesting observations have been made by George and Elizabeth Peckham ('98, pp. 211-219) on the sense of direction in the solitary wasps. When the wasp starts out from its nest, it flies quite around it and gradually circles farther and farther away in a constantly enlarging spiral, sometimes recrossing its path a number of times. The authors' observations show that this action is to enable the wasp to familiarize itself with its surroundings, so that it can find its way home when it so desires. The similar phenomenon observed in other insects, such as ants, is, no doubt, for the same purpose. Davenport ('97, pp. 278-279) in his experiments on *Amoebae* found that, when their movement was undirected by any external stimulus, they tended to travel in curious spiral loops. Pouchet ('72, pp. 227-228) made observations on the movement of larvae of *Musca* (*Lucilia*) *caesar* in the dark. There is a striking contrast between the paths given by him of the undirected movements and those made in response to the stimulus of light. The tendency to travel in a gradually widening spiral has also been observed by the writer in young frog and toad larvae — before the development of mouth and eyes — when they are dislodged from the support to which they are clinging.

Most of the following experiments on the slug were made in a room about 12 feet square. The floor was sometimes covered with cardboard or paper, but in other experiments was left bare. Heavy curtains were hung in front of the windows and light shut out as completely as possible. The experiments were conducted at night, and the temperature of the room was nearly, if not quite, constant. A slug was put on the floor in the centre of the room and left to itself for two or three hours, sometimes longer. By means of the mucous secretion, which hardened into white, shiny flakes, the exact path of the animal could, in most cases, be easily followed. This path was roughly reproduced by pencil on paper. A number of these paths are given in Figures 3-22, much reduced from the actual space covered. The series here given includes all the animals experimented on, with the exception of three individuals which did not



FIGURES 322.

Much reduced copies of the tracks made by slugs (*Limax maximus*) in the dark.
 dx., right-handed loops ; s., left-handed loops.

give any characteristic paths. Two of the three moved only a short distance in wavy lines without recrossing their paths, and were in poor condition, for they did not go far, and shortly died. One extremely active little individual moved ahead in a straight line quite across the floor, a distance of eight or ten feet. With these few exceptions, it will be seen that there is a very marked tendency to travel in loops. In general, the loops varied in size from a couple of inches in diameter to two feet and sometimes more. The animal generally makes a circle soon after starting out, and then may travel for some distance before again recrossing its tracks. The individuals which did the most looping also showed a tendency, by gradually swinging away from the starting point, to make larger and larger circles. Nos. 7, 8, 11, 13, 14, 16, 17, 19, and 22 all showed this tendency. The smaller individuals usually make the smaller loops, but this is not always the case. Although the paths made by different animals have a very different appearance, they all show the same general looping tendency. It will at once be noticed that all curves are not in the same direction. Some are right-handed loops, others are left-handed, and two cases, Nos. 10 and 12, contain loops of both right and left hand character, or at least indicate a tendency to the formation of such loops. As a rule, however, the individual shows a marked constancy in the character of the loops made. Disregarding the two cases in which there were both right and left hand loops, we have ten individuals with a tendency to circle to the right and eight individuals with just as marked a tendency to circle to the left. This does not indicate a very great preponderance of individuals travelling to the right. If the total space travelled over by all individuals be considered, I think it might show, on the average, a more marked swerving to the right than does a counting of right and left circling individuals, but I have not measured the distances carefully enough to speak confidently on this point. The evidence thus far accumulated in regard to an asymmetrical response of the right and left sides to artificial stimuli points to a greater sensitiveness of the left side, which is perhaps correlated with a *slight* average tendency to move toward the right side more than to the left.

SUMMARY OF PART III.

These studies on the light responses of *Limax maximus* seem to establish the following points:—

- (1) The animals are markedly phototactic.
- (2) There are individual differences in phototaxis, as there are in geotaxis.

(3) To strong light, slugs, on the average, give a strong negative response.

(4) The degree of response gradually diminishes with the reduction in the strength of the stimulus.

(5) There is a certain strength of light which appears neither to repel nor attract the slug. This may be said to be a neutral stimulus.

(6) Reduction of the intensity of the light beyond the neutral point changes the phototaxis from negative to positive.

(7) The positive response becomes stronger up to a certain degree of intensity.

(8) It then gradually diminishes with decreasing intensity until absolute darkness accompanied by no response is reached.

(9) Slugs are responsive to light stimuli covering a wide range of intensities.

(10) The principal organ of response is probably the eye.

(11) The response is unsymmetrical on the part of the right and left sides of the animal's body. The right side is not as sensitive to stimuli as is the left. On the whole the right side moves through a slightly greater arc in a period of 45 seconds than does the left.

(12) In the dark, other directive stimuli being eliminated, the slug tends to travel in a spiral of gradually increasing radius, though almost invariably producing one or more loops. Some slugs make right-hand loops, others left-hand ones; there is a slightly greater tendency to right-hand circling.

These responses of the slug to touch, gravity, and light-stimuli emphasize the fact that it is an animal's normal environmental conditions which chiefly determine its general response to artificial stimuli. The variations in precision and character of this general response are mainly dependent on certain internal factors, such as the food conditions of the animal, its fear of an enemy, and desire to escape captivity.

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